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Impacts of Hydroelectric Dams on Aquatic Macroinvertebrate Oviposition Strategies: The Role of Desiccation

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IMPACTS OF HYDROELECTRIC DAMS ON AQUATIC MACROINVERTEBRATE OVIPOSITION STRATEGIES: THE ROLE OF DESICCATION

by

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Abstract:

Previous studies quantifying the density, distribution and diversity of aquatic insects overwhelmingly focus on larval life stages. However, many aquatic insects exhibit selective oviposition behaviors, with a preference for emergent substrates along a river's edge. The practice of hydropeaking creates an artificial intertidal zone that is absent from natural rivers and to which freshwater organisms are not adapted. We hypothesized that this novel disturbance could reduce the availability and temporal persistence of oviposition habitats resulting in egg mortality. To test this hypothesis, we quantified the oviposition behavior of four aquatic insects using a hierarchical field survey of habitat availability and utilization. We found that three out of four genera exhibited preferences for larger, emergent substrates located along the river edge, thus increasing the likelihood of desiccation during stage height fluctuations. When subject to experimental drying, we observed up to 93% egg mortality during desiccation lasting two hours or less, and 100% mortality when desiccation exceeded four hours. These paired field and experimental results suggest that hydropeaking could impart a population bottleneck on aquatic insects. This project is on-going and these writing do not reflect the final views of the authors.

Title: Oviposition habitat selectivity and egg mass desiccation tolerances of select aquatic insects in a tailwater ecosystem: implications for population dynamics in large regulated rivers

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Introduction

It is widely recognized that large rivers are among the most anthropogenically impacted ecosystems on Earth (Allan and Flecker 1993, Dynesius and Nilsson 1994, Carpenter et al. 2011). Rivers have long been valued by human societies as sources of drinking water, aquaculture, waste disposal, transportation, recreation, and energy production (World Commission on Dams 2000, Kennedy et al. 2016). The construction and management of large dams may be among the most ubiquitous impacts, with an estimated 800,000 dams worldwide (Richter and Thomas 2007), and a mere 2% of the United States' rivers maintain unaltered hydrologic regimes (Graf 1993). Dam construction and management can negatively impact downstream ecosystems, known as *tailwaters*, by altering hydrologic, sediment, and thermal regimes, as well as by imposing significant migration barriers to aquatic organisms (Poff et al. 2007, Schmidt and Wilcock 2008, Olden and Naiman 2010, Dugan et al. 2010).

Power generation is a core function of dams worldwide, with an estimated 20% of global power supplied by hydroelectricity (World Commission on Dams 2000, Zarfl et al. 2015). Hydropeaking and load following flows are common water release strategies used to meet daily peak power needs and to maximize the market value of produced power (García et al. 2011, Førsund 2015, Kennedy et al. 2016). Under these scenarios, the magnitude of daily discharge fluctuates to coincide with peak energy demand, with either a single long-duration peak or two

short-duration peak discharge events occurring daily (i.e., *double-peaking*). In either scenario, hydropeaking operations can substantially increase daily hydrologic variability (Cushman 1985, Gore et al. 1994), which can alter downstream algal, macroinvertebrate, and fish assemblages (Moog 1993, Blinn et al. 1995, Young et al. 2011, Miller and Judson 2014). For example, Blinn et al. (1995) found that hydropeaking led to significant reductions in both green algae and macroinvertebrate biomass within hydrologically variable shoreline habitats of the Colorado River below Glen Canyon Dam compared to the permanently wet main channel. Despite extensive study of ecological impacts to downstream organisms, the specific mechanisms by which hydropower production alters tailwater community composition are uncertain.

The novel environmental conditions resulting from dam construction and management can be particularly deleterious to disturbance adapted populations having evolved life history strategies optimized to survive and even exploit natural disturbances (reviewed in Lytle and Poff 2004). This is particularly true for aquatic insects having complex life cycles that typically require both aquatic (larvae, pupae, eggs) and terrestrial (adult) life stages. The dependence of aquatic insects on both aquatic and terrestrial habitats means they can be subjected to novel conditions created by altered flows as both aquatic larvae and terrestrial adults returning to complete their life cycle. Previous studies have disproportionately focused on aquatic larvae Downes and Reich 2008, *citations*), but recent evidence suggests that environmental alterations impacting other life stages such as adult or egg could be equally important for population dynamics (Kennedy et al. 2016). For example, studies have demonstrated that additions and reductions of preferred adult egg-laying, or oviposition, habitat from small stream reaches correlate to significant increases and decreases, respectively, in the abundance of both egg masses (Encalada and Peckarsky 2012, MacQueen and Downes 2015) and larvae (Encalada and

47 Peckarsky 2012, Lancaster and Downes 2014). Furthermore, certain caddisfly egg mass
48 morphologies have been shown to reduce deleterious effects of high flows and predation,
49 potentially increasing survivorship of new larvae (Bovill et al. 2013, Bovill et al. 2014).
50 However, these studies have largely addressed life history responses to natural disturbance
51 regimes in small streams and not novel environmental conditions such as those resulting from
52 hydropower production in large, tailwater environments.
53 The potential for altered flows to influence non-larval insect life stages remains vastly
54 underexplored. Only recently have researchers proposed that insect population viability could be
55 limited by recruitment (the number of juveniles added to a population) constraints imposed by
56 hydropeaking operations on large rivers (Encalada and Peckarsky 2012, Bovill et al. 2013,
57 Kennedy et al. 2016). Hydropeaking operations can create artificial intertidal zones along
58 shorelines, known as varial zones, which are rare in naturally flowing rivers (Benenati et al.
59 1998, Blinn et al. 1995, Kennedy et al. 2016). If flow fluctuations due to hydropeaking are
60 frequent and severe, the varial zone can alternate between wet and dry phases on a daily basis,
61 becoming a harsh environment for tailwater organisms that use shoreline habitats during one or
62 more life stages. Since most adult tailwater insects are believed to preferentially oviposit on
63 emergent substrates located within the varial zone (Kennedy et al. 2016), intra- and inter-daily
64 water level fluctuations from hydropeaking could influence recruitment by altering the spatial
65 and temporal availability of optimum oviposition habitats or by desiccating eggs cemented to
66 benthic substrates. Specifically, rising water levels can act to submerge suitable emergent
67 substrates along the shoreline, while receding waters can essentially remove these substrates
68 from the confines of the wetted channel. Additionally, cemented egg masses laid at artificially
69 high stage heights can become stranded when water levels retreat, increasing the risk of

desiccation-induced mortality. If hydropeaking flows create unfavorable environmental conditions that reduce or prohibit successful oviposition, egg hatching, or both, population bottlenecks could occur, potentially changing assemblage composition and ecosystem function.

The goal of this study was to examine hydropeaking-induced mechanisms that affect processes at non-larval insect life stages, specifically adult oviposition habitat selectivity and egg mass desiccation. We used a combination of benthic particle surveys and artificial substrate deployments to determine preferred oviposition habitats, and hypothesized that adult tailwater insects would differentially oviposit on emergent mineral substrates located in the varial zone.,With oviposition habitat preferences identified, we then asked if daily water level fluctuations from hydropeaking alter the availability of preferred habitats, and whether egg masses in these habitats were at greater risk of desiccation-induced mortality due to chronic atmospheric exposure. To investigate the role of desiccation, we subjected egg masses of three insect taxa to various durations of atmospheric exposure in the lab and monitored the subsequent hatching success of individual egg masses. We predicted that hatching success rates would vary as a function of exposure time and egg mass morphology, with gelatinous egg masses possessing the greatest desiccation tolerance. Information obtained through this study will inform the adaptive management of hydropower operations to better balance societal power demands with the integrity of aquatic insect population dynamics and community composition in large tailwater ecosystems.

Methods

Study area

92 This study was conducted within a 27 km section of the Green River below Flaming
93 Gorge Dam (FGD), near Dutch John, Utah, USA (Fig. 1). The Green River originates in the
94 Wind River Mountains in Wyoming, USA, and flows south through Wyoming, Colorado and
95 Utah. The Green River is the largest tributary of the Colorado River, and is historically
96 characterized by a snowmelt hydrologic regime with maximum flows occurring in the spring,
97 and relatively stable base flows dominating the remainder of the year. The completion of FGD in
98 1963 (4.67×10^9 cubic meter storage capacity relative to mean annual flow of 52 m^3 sec^{-1})
99 significantly altered the hydrology of the river by reducing the mean annual peak flow, altering
100 the seasonal timing of high and low flow events, increasing base flows and increasing intra-daily
101 variation due to hydropeaking for electrical power generation (Vinson 2001, Miller et al. 2013).
102 The direct and indirect effects of hydrologic alteration resulted in the extirpation of over twenty
103 macroinvertebrate species, with the present day tailwater supporting a depauperate invertebrate
104 fauna dominated by *Hyallela azteca*, Chironomidae *spp.*, *Simulium* sp., *Gammarus lacustris*,
105 Oligochaeta, and *Baetis* spp. (Vinson, 2001).
106
107 *Study organisms*
108 We characterized the oviposition habitat selectivity of four Green River tailwater insect
109 taxa: *Baetis* spp. (Ephemeroptera), *Hydropsyche occidentalis* (Trichoptera), *Brachycentrus*
110 *occidentalis* (Trichoptera), and Chironomidae (Diptera). For all taxa but Chironomidae, we also
111 quantified egg mass desiccation tolerance. These taxa were selected because they are thought to
112 exhibit differential oviposition strategies (e.g., edge versus deep-water specialists, landing on
113 versus swimming to oviposition substrates), possess differing egg mass morphologies (e.g.,

114 gelatinous versus non-gelatinous, flat versus spherical; see descriptions below), and they are
115 common in large, western U.S. rivers.

116 *Baetis* spp. mayflies (hereafter, *Baetis*) are ubiquitous aquatic insects with extensively
117 studied oviposition behaviors (Eaton 1888, Morgan 1911, Elliot 1972, Peckarsky et al. 2000,
118 Peckarsky et al. 2001, Peckarsky et al. 2002). Populations in the Green River are bivoltine, with
119 an overwintering larval generation that emerges and reproduces as adults throughout April and
120 May, and a summer generation that emerges and reproduces between September and October.
121 Previous studies in other systems have observed that *Baetis* spp. exhibit highly specialized
122 oviposition behaviors where adult females will land on large, emergent rocks and then crawl on
123 the downstream side to oviposit a single egg mass under water on the rock's ventral surface
124 (Eaton 1888, Peckarsky et al. 2000, Encalada and Peckarsky 2006). Each *Baetis* egg mass
125 contains hundreds to thousands of eggs laid in rows to form a single, flat layer that resembles the
126 shape of a tombstone and is only protected by a thin chorion (Fig. 2).

127 *Hydropsyche occidentalis* is a free-living, filter-feeding caddisfly common in rivers and
128 streams of the western U.S. Green River populations are univoltine, with prolonged adult
129 emergence occurring during summer and fall months (June – October). As observed in other
130 caddisflies (Lancaster et al. 2010b), adult female Hydropsychids swim through the water column
131 to oviposit on the undersides of submerged substrates, sometimes exceeding four meters in depth
132 (Deutsch 1984). *H. occidentalis* egg masses are similar to those of *Baetis* in that they are
133 arranged in a single, non-gelatinous layer of several hundred eggs cemented to a substrate's
134 ventral surface (Fig. 2). However, egg masses of *H. occidentalis* are more irregular in shape, and
135 individual eggs are larger.

136 *Brachycentrus occidentalis* is a case-building, filter-feeding caddisfly that occurs
137 throughout running waters of western North America. Previous studies indicate that populations
138 of *B. occidentalis* are univoltine with adult emergence occurring mostly in spring and early
139 summer (Wiggins 1996, Gallepp 1974). While it is unclear how adult females reach oviposition
140 sites, we observed egg masses of this species cemented below the water line on the lateral and
141 near-ventral edges of emergent particles. Egg masses of *B. occidentalis* are unique compared to
142 those of *Baetis* or *H. occidentalis* in that masses are spherical, and individual eggs are embedded
143 within a gelatinous matrix (Fig. 2), which was absent from all other egg mass types in this study.
144 Non-biting midges in the family Chironomidae are worldwide in distribution and often
145 contribute significantly to the energetics of aquatic ecosystems and surrounding landscapes due
146 to short life cycles and high biomass (Merritt et al. 2008). Chironomids emerge year-round on
147 the Green River, though the majority of adults are found in spring and summer months (M.
148 Schroer, personal observation). During our study, adult females were observed to land on
149 emergent rocks and crawl to the water, where they would lay egg masses (often en-masse)
150 primarily along the downstream edge at the water surface elevation. Sampled egg masses, known
151 as ropes, consisted of hundreds to thousands of rod shaped eggs arranged in spiraled strings (Fig.
152 2). We were unable to distinguish among egg masses of different midge species, but examination
153 of pupal exuviae collected during surveys and larval taxonomic records indicate that four genera
154 accounted for most egg masses in this study: *Diamesa*, *Eukiefferiella*, *Tvetenia* and the
155 *Cricotopus/Orthocladius* complex.
156
157 *Oviposition habitat surveys*

158 To quantify oviposition habitat availability and selectivity, we conducted substrate
159 surveys in 2015 and 2016. We used personal observations and communication with local fishing
160 guides to identify periods of peak insect emergence and subsequent oviposition. We focused on
161 three sites below FGD: Tailrace (1 kbd), Grasshopper Island (14 kbd), and Indian Crossing (26
162 kbd), hereafter referred to as S1, S2, and S3, respectively. These sites were selected to represent
163 geomorphic and hydrologic gradients below FGD, particularly the interaction of width:depth
164 ratios and the magnitude of intra-daily stage height fluctuations resulting from hydropeaking. For
165 example, S1 is located in a deep bedrock canyon where bankfull widths range from 40 – 150 m
166 and base flow water depth from 1 – 10 m. Bed material in riffles consists of coarse gravel,
167 cobbles and boulders. In this river section, the canyon bound morphology results in the greatest
168 stage height fluctuations during periods of hydropeaking. In contrast, S3 is located in alluvial
169 plains of Brown's Park where bankfull widths increase to 200 m, base flow water depths
170 decrease to an average of 0.5 – 2 m and bed material grades from gravel and cobble to seasonal
171 deposits of sand and silt exported from Red Creek located upstream (Vinson, 2001).
172 We employed a hierarchical sample design to characterize oviposition habitat availability
173 and use. Using aerial photography, a single 1.5 km river segment was chosen to be representative
174 of the geomorphic diversity within each of the three sites. Two fast-water (i.e., riffles) and two
175 slow-water (i.e., runs) reaches (maximum length = 75 m) were randomly selected for sampling
176 for a total of four reaches per 1.5 km segment. The three river segments (12 reaches total) were
177 sampled on multiple occasions during summer of 2015 and spring of 2016. To control for
178 changing daily water levels due to hydropeaking, surveys across all sites and reaches were
179 conducted at the lowest day time discharge, which were 51.0 and 22.7 $m^3 s^{-1}$ for summer 2015
180 and spring 2016, respectively.

181 Observations from past studies (Peckarsky et al. 2000, Hoffmann and Resh 2003,
182 Lancaster et al. 2010a and 2010b), as well as a pilot study below FGD, indicate that egg masses,
183 in general, are disproportionately found on emergent rocks or woody substrates in moderate
184 water velocities, often near river margins. As these habitats are not present in equal proportions
185 from reach to reach or segment to segment, a simple random sample would result in under-
186 sampling some habitats (e.g., emergent rocks or vegetation) and oversampling others (e.g.,
187 submerged rocks). Therefore, to characterize both available and selected oviposition habitats
188 (also interchangeably referred to as substrates and particles), we followed Reich and Downes
189 (2003) and utilized a two-stage sample design. In the first stage, referred to as random surveys,
190 reaches were sampled using a random-systematic approach to characterize substrate availability,
191 as well as the physical characteristics of substrates. Specifically, 10 points were sampled along
192 each of five transects for a total of 50 points per reach. Transects were located using a random
193 starting point within each reach and then systematically spaced at regular intervals. Transects
194 were oriented perpendicular to the channel and extended to mid-channel or a depth of 1 m for
195 safety reasons. Lastly, the 10 points per transect were not equally spaced, with the first five
196 particles spaced at 0.5 m intervals to measure more rapid physical changes along channel
197 margins. The remaining five particles were spaced at regular intervals to mid-channel or a depth
198 of 1 m, whichever cam first.
199 The second sampling stage, referred to as *stratified surveys*, involved the stratification of
200 sample reaches by substrate type for a total of five possible strata: 1) submerged rocks, 2)
201 emergent rocks, 3) submerged wood, 4) emergent wood and 5) emergent vegetation. To achieve
202 minimum sample sizes among strata (n = 15), up to 15 additional random points were sampled
203 per strata per reach (note that the 50 random points used to quantify substrate availability in stage

204 one counted towards the substrate counts in the respective strata). In total, we sampled between
205 75 – 110 points per reach for a total of 300 – 440 points per 1.5 km segment, depending on the
206 number of strata present per reach.

207 At each of the 75 – 110 points per reach, the following parameters were measured: reach
208 type, distance from bankfull, particle type, particle size, particle depth, emergent area, water
209 velocity, embeddedness and the type and abundance of egg masses (Table 1). The aggregated
210 morphology of Chironomidae egg masses precluded direct enumeration, so we developed an
211 ordinal scale based on aerial extent of the substrate covered by egg masses. If midge egg masses
212 were present, the area of substrate covered by all masses was estimated to be less than the area of
213 either a standard US postal stamp (2.2 x 2.5 cm), credit card (5.4 x 8.5 cm), standard envelope
214 (10.5 x 24.0 cm) or an 8.5 x 11 inch sheet of paper (21.5 x 27.9 cm) (Table 1). For all other taxa,
215 egg abundances were categorized as: 1 – 10, 11 – 50, 51 – 100 and > 100 egg masses per rock.
216
217 *Artificial oviposition substrates*

218 To validate our observational study of oviposition habitat preferences, we experimentally
219 manipulated particle depth (i.e., emergent versus submerged) and distance from bankfull in two
220 separate trials. We focused on these two environmental factors because they form the basis for
221 hypotheses related to hydropeaking and egg viability, they were among the top predictors in
222 habitat selectivity models and they were easily manipulated. Specifically, we used 20 x 20 x 20
223 cm cinderblocks as artificial substrates for oviposition. Blocks were arranged in five transects,
224 with four replicates per transect. The five transects were oriented parallel to the river bank and
225 located approximately 3.0, 4.5, 7.5, 10.5 and 13.5 m from the bank.

226 The first trial was run with all emergent blocks and the second all submerged. Combined,
227 these two experimental trials allowed us to test for differential use of emergent versus submerged
228 particles and whether use depended on distance from bankfull. For the submerged treatment, we
229 also included an emergent control to ensure oviposition was actively occurring. Trials were run
230 consecutively in March and April of 2016, and each trial lasted for 7 – 17 days to allow
231 sufficient time for adults to oviposit on blocks. At the beginning and end of each trial, we
232 recorded distance from bankfull (m) and particle depth (cm) for each of the 20 artificial
233 substrates. At the end of each trial, substrates were retrieved and checked for egg masses of
234 *Baetis* and Chironomidae. *H. occidentalis* and *B. occidentalis* egg masses were not found on
235 artificial substrates in sufficient numbers for analysis.
236
237 *Hydropeaking effects on optimal oviposition habitats*
238 We used differences in baseflow discharge between years (2016: 51.0 $m^3 s^{-1}$ and 2015:
239 22.7 $m^3 s^{-1}$) to understand how emergent substrate availability varies with stage height
240 fluctuations; the difference in discharge between years was equivalent to the stage height
241 fluctuations associated with hydropeaking for 2015. Specifically, for each of the three segments,
242 we calculated the average number of emergent rocks and compared the values between years.
243 We chose to examine emergent rocks, as these proved to be highly preferred substrates for
244 *Baetis*, *B. occidentalis* and Chironomidae.
245
246 *Desiccation tolerances of egg masses*
247 To determine desiccation tolerances of insect eggs, we exposed egg masses to a single
248 drying event of varying duration and measured the hatching success of each mass. Egg masses

249 were collected from the Green River using both natural and artificial substrates (slate tiles
250 attached to cinder blocks). Egg masses and/or slate tiles were removed from substrates, placed in
251 Whirlpak® bags filled with river water, stored on ice and transferred to the lab. Within 24 hours
252 (h) of collection, we placed egg masses into individual petri dishes filled with chlorine-free water
253 and assigned egg masses to one of six desiccation treatments: 0, 0.5, 1.0, 2.0, 4.0 or 8.0 h in a
254 completely randomized factorial design. Treatment levels greater than 2.0 h represent common
255 durations for varial zone exposure below hydropeaking dams, while treatment durations less than
256 2.0 h were added to understand general insect desiccation tolerances. The number of replicates
257 per treatment depended on egg mass availability and ranged from 14-16 (total n = 84, 96 and 90
258 for *Baetis* spp., *H. occidentalis* and *B. occidentalis*, respectively). Results from Chironomidae
259 desiccation trials are only anecdotally presented in the discussion due to difficulties in
260 enumerating the total number of eggs per mass.
261 After each treatment, egg masses were rehydrated, photographed under a dissecting
262 microscope and reared at approximately 23°C under an artificial light regime of 12 h light:dark.
263 The total number of eggs per mass was estimated using Image J© software, or counted directly
264 in the case of *H. occidentalis*. Water was renewed in each petri dish every 24 – 48 h in an effort
265 to maintain dissolved oxygen levels and to reduce potential for fungal or bacterial growth. We
266 checked egg masses every 2 – 3 days for hatched larvae, which were counted and removed. An
267 individual was considered "hatched" if it showed evidence of physical development beyond the
268 embryo stage (e.g., formation of sclerotized plates or uncurling of abdomen). Experiments ran
269 for a total of 4 – 7 weeks and were terminated when the cumulative number of hatched
270 individuals counted across all treatments on a given day fell below 1.0% of the total number of
271 hatched individuals for the experiment to date. For all experiments, desiccation tolerance was

interpreted from hatching success, defined as the ratio of hatched individuals to the total number of eggs per mass.

Statistical analyses

We used Random Forest (hereafter, RF) models fit in R (package 'randomForest', version 3.4.1, R Development Core Team 2017) to quantify the relationship between egg mass abundance and environmental variables at segment, reach and substrate particle scales. Year was not a significant factor in any models and thus data from 2015 and 2016 was combined into a single model per species with egg abundance as the response variable. RF is a tree-based approach that fits thousands of classification or regression trees to a dataset where individual trees are developed for a bootstrapped sample of the data using a random subset of predictors at each split to find the most homogenous groups (Breiman 2001, Liaw and Wiener 2002). Model performance was assessed using percent variance explained, which is an internal cross validated metric defined as 1 – (mean squared error)/(variance(response)), and is analogous to r-squared (Pang et al. 2006). Variable importance was assessed using percent increase in mean square error (MSE) following the permutation of individual predictor variables, with higher MSE values indicating a greater decrease in model accuracy (Pang et al. 2006). Partial dependence plots were constructed to assess the relationship of individual predictors to the response variable by holding the effects of all other predictors in the model constant (Cutler et al. 2007).

For artificial substrates we tested for differences in egg mass abundance as a function of distance from bankfull (five levels: 3.0, 4.5, 7.5, 10.5 and 13.5 m) using a generalized linear model (GLM) in R ('glm' function in the package 'stats', version 3.4.1). Models were built using a poisson distribution and log link function and run separately for each of *Baetis* spp. and

295 Chironomidae. *H. occidentalis* and *B. occidentalis* were not found in sufficient numbers for
296 analysis and no formal models were run for tests of egg abundance differences between emergent
297 and submerged particles, as only one of 20 submerged particles contained eggs.
298 GLM models were also used to test for differential hatching success among
299 desiccation treatments. Specifically, models were built using a quasibinomial distribution and
300 logit link, where a quasibinomial distribution was used to mitigate the effects of over-dispersion.
301 Significant overall model results were followed by Tukey post-hoc test to determine the exact
302 duration of desiccation that resulted in a significant decline in hatching success. This analysis
303 allowed us to determine critical desiccation threshold ranges and emphasize the importance of
304 different egg morphologies.
305
306 **Results**
307 *Egg mass abundance and distribution patterns*
308 We enumerated 5527 egg masses among the three study segments with *Baetis* having the
309 greatest number (2606) followed by *B. occidentalis* (2152), Chironomidae (492) and *H.*
310 *occidentalis* (277). *H. occidentalis* and *B. occidentalis* egg masses were only found during late
311 June and July sampling events, while *Baetis* and Chironomidae were found throughout spring
312 and summer months, with higher abundances in spring than summer. Egg mass abundances
313 generally differed among segments; *H. occidentalis* egg mass abundances increased with
314 distance downstream and *Baetis* and Chironomidae abundances decreased (Fig. 3). Egg mass
315 abundances were consistently higher in fast water reaches compared to slow water, with
316 downstream abundances of *Baetis* being the one exception.
317

318 *Oviposition habitat selectivity*

319 Preferred oviposition habitats of all four taxa were not randomly distributed, but rather
320 differentially located within reaches and across substrate types. RF model precision was 68% for
321 Chironomidae, 52% for *B. occidentalis*, 43% for *Baetis* and 20.8% for *H. occidentalis*. The
322 relative importance of the nine predictor variables was similar among models, with measures of
323 particle size, type and emergent area, distance from bankfull, particle depth and segment among
324 the top predictors (Fig. 4). In general, all four taxa preferred large and/or emergent particles (Fig.
325 5). *Baetis*, *B. occidentalis* and Chironomidae appear to be edge specialists, preferring large
326 emergent particles located close to the bank or in otherwise shallow waters, while *H. occidentalis*
327 utilized mostly large particles located in deeper water (Fig. 6). Notable differences among
328 models included the strong influence of water velocity for *Baetis* and *B. occidentalis* and to a
329 lesser extent, differences among segments for *Baetis*, *H. occidentalis*, and Chironomidae.
330
331 *Artificial oviposition substrates*

332 We observed similar particle preferences for *Baetis* and Chironomidae during
333 experimental manipulations of particle depth and distance from bankfull. Oviposition almost
334 exclusively occurred on emergent particles, with only one of 20 submerged particles containing
335 eleven *Baetis* egg masses. Chironomidae adults laid eggs on emergent cinder blocks only – no
336 egg masses were found on submerged blocks. Given the paucity of egg masses on submerged
337 particles, we compared egg abundances as a function of distance from bankfull for only
338 emergent particles. *Baetis* egg mass abundances significantly differed among transects (χ^2 =
339 40.6, df=3, $p < 0.001$), with the two closest transects having the highest abundances and
340 significantly lower abundances for transects located 7.5 and 10.5 m from bankfull. In contrast,

341 we observed no differences in Chironomidae egg mass abundance with distance from bankfull
342 ($\chi^2 = 0.62$, $df=3$, $p = 0.891$).
343
344 *Hydropeaking effects on optimal oviposition habitats*
345 We observed reductions of 37, 88 and 100% in the average number of emergent rocks per
346 segment found during random surveys conducted at 50.97 and 22.65 $m^3 s^{-1}$ among S1, S2 and
347 S3, respectively (Fig. 7). Reductions in the number of emergent rocks increased with distance
348 downstream as mean particle size decreased; the mean particle size of emergent rocks found
349 during random surveys decreased from 524 mm at S1 to 302 mm at S3.
350
351 *Desiccation tolerances of egg masses*
352 All three taxa exhibited reductions in hatching success in response to desiccation,
353 although the duration of desiccation corresponding to the greatest declines differed among taxa
354 (Fig. 8). *Baetis* exhibited the lowest desiccation tolerance, followed by *H. occidentalis* and then
355 *B. occidentalis*. The hatching success of *Baetis* significantly differed among treatments ($\chi^2 =$
356 3013.9, $df=3$, $p < 0.001$), with significant declines starting after one hour of desiccation ($\beta = -$
357 4.32, $z = -3.37$, $p = 0.003$). On average, eggs masses desiccated for 0.0 h were 37% more likely
358 to hatch than eggs desiccated for 1.0 h. *Baetis* treatments lasting longer than 2.0 h resulted in
359 100% egg mortality (Fig. 8).
360 We observed 100% egg mortality in both the 4.0 and 8.0 h treatments for *H. occidentalis*,
361 while a single individual hatched across all 2.0 h replicates. In contrast, there was no evidence of
362 differences in hatching success among the control, 0.5 and 1.0 h treatments ($\chi^2 = 7.6$, $df=2$, $p =$
363 0.839).

364 Egg masses of *B. occidentalis* were the most tolerant to desiccation. We observed
365 significantly different hatching success among treatments ($\chi^2 = 355.8$, $df=5$, $p < 0.026$), but no
366 significant differences were observed for pair-wise comparisons to the control.
367
368 **Discussion**
369 Aquatic insect assemblages have been shown to be depauperate below hydroelectric
370 dams in comparison to unaltered systems; however, the exact mechanisms for population
371 declines has eluded researchers. We provide evidence for a novel hypothesis related to egg
372 recruitment limitations resulting from hydroelectric dam operations. Specifically, we found that
373 adult tailwater insects generally prefer to oviposit on large, emergent particles located along
374 river's edge, and that fewer of these preferred substrates are present within segments at higher
375 flows commonly associated with hydropeaking. Additionally, we observed high mortality rates
376 to short duration desiccation events highlighting the susceptibility of egg masses subject to
377 fluctuating flows and subsequent atmospheric exposure. Below we discuss these results and
378 highlight two mechanisms by which hydroelectric dam operations have the potential to limit
379 insect population recruitment.
380
381 *Oviposition habitat selectivity*
382 Researchers have long suggested that organisms select habitats using a hierarchical
383 process, whereby decisions are made at several nested spatial scales (Hildén 1965, Orians and
384 Wittenberger 1991, Wildermuth 1994). Hoffmann and Resh (2003) provided early evidence of
385 hierarchical oviposition habitat selection for aquatic insects in small streams, showing that
386 females of two caddisfly species use cues at three different spatial scales, from the stream reach

387 down to the scale of individual substratum, to determine an oviposition site. We found similar
388 support for hierarchical habitat selection by ovipositing insects in a large western US tailwater.
389 Results from our surveys suggest that most female adults use cues at segment, reach and
390 substratum scales (see methods) to determine optimal oviposition habitats. Specifically, adults
391 largely prefer to oviposit on emergent particles located along a river's margin in fast-water
392 reaches.

393 At the segment scale, adults appear to specifically target faster flows, as the vast majority
394 of all egg masses surveyed were found in fast-water reaches (Fig. 3). Adults likely use polarized
395 light from faster moving water to cue in to these areas (Schwind 1991, Kriska et al. 1998), and
396 hypotheses as to why these flows are targeted include better dispersal capabilities for hatched
397 larvae, more reliable oxygen delivery to egg masses and mitigation against fine sediment build-
398 up (Hoffmann and Resh 2003, Lancaster et al. 2010b). Faster waters may also provide some
399 protection against receding water levels, as faster moving water is more likely to induce
400 splashing, which could act to distribute small amounts of water to additional areas and maintain a
401 moist environment for egg masses left exposed above water line after flows recede.

402 Once a reach has been chosen, insects in this study overwhelmingly oviposited on
403 substrates located in the varial zone near water's edge. *Baetis*, *B. occidentalis*, and Chironomidae
404 all exhibited strong edge-specialist oviposition behaviors (Fig. 6 Panels XYZ). Only *H.*
405 *occidentalis* showed some preference for substrates located more mid-channel (Fig. 6 Panel X).
406 Egg masses of edge-specialists were found aggregated in high numbers on substrates located
407 within 5 m of bankfull, while substrates located outside the varial zone contained significantly
408 fewer egg masses. Though a causal basis for preferring substrates located nearer to shore has yet
409 to be demonstrated, it is thought that this behavior may reduce predation risk for adult females

410 (Lancaster et al. 2010b). Adult tailwater insects are often found in riparian vegetation or flying in
411 mating swarms along a river's edge, so ovipositing on substrates closer to these environments
412 reduces the distance an adult female must travel, in turn reducing costs to fitness and the chances
413 of predation. Additionally, substrates found in mid-channel are often located in deeper water,
414 requiring an adult female with cementing oviposition behavior to swim or crawl a further
415 distance to reach the optimal area of a substrate, increasing chances to be predated upon or swept
416 downstream in the current. Perhaps the simplest explanation for this result in large rivers,
417 however, is that the largest proportion of favored habitat (i.e., emergent particles, see below) is
418 naturally located in shallower water near shore. Additional research is warranted to further
419 explore this selective behavior.

420 At the scale of individual particles, several substrate characteristics were consistently
421 ranked as top predictor variables across all study taxa – most notably particle size, particle type
422 and emergent area (Fig. 4). All study taxa showed preferences for larger particles (Fig. 5).
423 Evolutionarily, this makes sense given that larger particles are less prone to disturbance by
424 catastrophic flows, which could damage egg masses (Encalada and Peckarsky 2006). It is also
425 thought that laying eggs on larger substrates may provide flow refugia for neonate larvae
426 (Hoffmann and Resh 2003). In addition to particle size, all study taxa exhibited preferences for
427 certain particle types. Edge-specialists all strongly preferred emergent particles, while *H.*
428 *occidentalis* targeted submerged particles (Fig. 6). Overall, emergent particles accounted for only
429 X% of all substrates sampled during random surveys, but accounted for Y% of substrates found
430 with egg masses present. This provides evidence that *Baetis*, *B. occidentalis*, and Chironomidae
431 are specifically targeting emergent particles for oviposition. Additionally, when egg masses were
432 found on emergent particles, ones with larger emergent areas were favored (Fig. 5). Larger

433 emergent areas may break up polarized light, helping females cue in to ideal substrates. They
434 may also serve as "landing pads" for adults to alight upon before crawling underwater to
435 oviposit. These results confirm our hypothesis that most adult tailwater insects are
436 disproportionately targeting preferred habitats in the varial zone for oviposition, despite their
437 relative short supply compared to other potential oviposition sites.

438 In contrast to edge-specialists that land and aggregate egg masses on emergent particles
439 within 5 m of shore, *H. occidentalis* females appear to swim through the water column to
440 oviposit on the undersides of submerged particles, including some located beyond 10 m.
441 Previous studies have documented this swimming behavior in other members of the
442 Hydropsychidae family (Fremling 1960, Rhame and Stewart 1976, Deutsch 1984). In this study,
443 *H. occidentalis* egg masses were found in low numbers - typically only 1 or 2 individual egg
444 masses - on submerged particles located in shallow water within 10 m from bankfull.
445 Accumulations of multiple egg masses were found on particles located in deeper water beyond
446 10 m, suggesting that these non-varial zone substrates were more preferred by females than
447 substrates located closer. It is important to note that we did not sample particles deeper than 1 m
448 for safety reasons, so it is quite possible that adults oviposited on particles located even further
449 away from shore than our results show, especially considering Deutsch (1984) observed
450 *Cheumatopsyche speciose* and *Hydropsyche phalerata* regularly swim 2-3 m to oviposit on the
451 riverbed of the Susquehanna River. This swimming behavior may help release *H. occidentalis*
452 from recruitment pressures amplified by hydropeaking operations (see below).

453 We believe results from our particle surveys are the first to empirically demonstrate that
454 tailwater insects strongly prefer to oviposit on particles found in varial zone environments.
455 Kennedy et al. (2016) concluded similar oviposition behaviors using trait databases for all

456 aquatic insects (Statzner and Beche 2010), but a formal test of these preferences was not
457 conducted. The oviposition preference results in our study are in line with previous studies from
458 smaller systems that have shown most adult insects to oviposit on large, emergent particles near
459 stream margins. While some adults lay their eggs directly into the water column (Encalada and
460 Peckarsky 2007) or within plants (Siva-Jothy et al. 1995), roughly 80% of aquatic insects with
461 known oviposition behaviors cement their eggs onto specific substrates (Statzner and Beche
462 2010, Kennedy et al. 2016). These substrates include wood (Hoffmann and Resh 2003,
463 MacQueen and Downes 2015), terrestrial and trailing vegetation (Hoffmann and Resh 2003) and
464 submerged and emergent rocks (Deutsch 1984, Peckarsky et al. 2000). Emergent rocks appear to
465 be especially important to several species of aquatic insects. Additionally, Lancaster et al.
466 (2010b) and Hoffmann and Resh (2003) also found evidence that certain species of caddisfly
467 (*Polycentropus flavomaculatus, Hydropsyche siltalai*, and *Hydatophylax* sp.) prefer to lay eggs
468 along stream margins.
469
470 *Artificial oviposition substrates*
471 Artificial substrate trials strongly corroborated results of our particle surveys that certain
472 tailwater insects overwhelmingly target emergent particles for oviposition. *Baetis* and
473 Chironomidae oviposition occurred almost exclusively on emergent blocks in experimental trials
474 When given the exact same substrate at varying distances from shore, adult *Baetis* oviposited on
475 the two near shore transects. In nature, *Baetis* females may lay eggs on substrates further out
476 from shore if other attributes of that substrate are appealing (size, flow, emergent area, etc.), but
477 when conditions are equal, habitats closer to shore are preferred. Although *Baetis* females
478 showed analogous patterns of oviposition in relation to distance from bankfull for both natural

and artificial substrates, midges oviposited equally across all transects in the artificial substrate trials, showing no apparent preference for blocks closer to shore. This is somewhat in contrast to results from particle surveys (Fig. 6) that showed a strong tendency for midges to lay egg masses on substrates located within 5 m from bankfull. However, it should be noted that bank distance was not as strong of a predictor variable for Chironomidae as compared to all other study taxa (Fig. 4). One possible explanation for this is that midges in this study were observed to lay eggs at the water surface elevation along emergent particles. In contrast, *Baetis* (as well as *H. occidentalis* and *B. occidentalis*) cement their egg masses well below water line. This behavior requires adult *Baetis* females to fully submerge themselves, which can increase the risk of predation by fish, as well as increase the risk of drowning or being swept downstream. Adults with submerging behaviors may decrease these risks by ovipositing on particles located in shallow waters near shore where velocities and shear stress are typically less severe. Our modeling results provide some additional support for this hypothesis, with water velocity being a more important predictor for Baetis (4^{th} out of nine predictors) than for midges (7^{th} out of nine predictors). Another explanation for midges using all transects includes the possibility that adult midge densities during the experimental trials and in the areas they were conducted were much higher than for our particle surveys. Higher oviposition densities could lead to over-saturation and use of sub-optimal habitats during the experimental trials. Nonetheless, results from artificial trials for both *Baetis* and Chironomidae reinforce the concept that many tailwater insects lay a large proportion of their egg masses on emergent particles in near shore environments.

Hydropeaking effects on optimal oviposition habitats

501 Stage-height fluctuations associated with hydropeaking have the potential to significantly
502 reduce the availability of optimal oviposition habitat on the Green River. We observed declines
503 in the average number of emergent rocks per segment between high and low water levels, and
504 the magnitude of these declines grew stronger moving downstream. The stark declines at S2 and
505 S3 make sense given changes in channel geomorphology and particle size. The Green River at
506 these sites is much wider and shallower as compared to S1, and average particle size declines
507 downstream (see methods and results). These smaller average substrates will be more easily
508 submerged by higher flows as compared to larger average particles found upstream.
509
510 *Egg mass desiccation tolerance*
511 Few studies have sought to quantify, compare or understand the importance of aquatic
512 insect egg morphologies, let alone test the potential effects of differing morphologies on
513 recruitment success and population dynamics. Recent studies involving desiccation have focused
514 on multivariate trait-based approaches to explain how macroinvertebrates can persist in arid
515 regions (Poff et al. 2006; Strachan et al. 2015) yet fail to demonstrate how variation in drying
516 time may influence their results. Our results suggest that egg morphology, specifically
517 spumaline, is a more significant factor for withstanding desiccating events than previously
518 thought. We consistently observed the greatest resistance to desiccation by taxa with the largest
519 volume of spumaline. For taxa with little to no spumaline, *Baetis* and *Hydropsyche,* 99% of eggs
520 were unable to hatch after a single 2 hour desiccating event. In contrast, *Brachycentrus* eggs
521 exhibited no significant change in hatching success after 8 hours of drying. Previous studies
522 have suggested that collateral coatings such as spumaline may protect eggs against predation,
523 parasitism, and desiccation (Hinton 1981, Hilker et al. 2008). Although few studies have

examined the chemical constituents of spumaline which may become increasing important for understanding the mechanisms driving tailwater community dynamics. Macroinvertebrates with spumaline coated eggs may be better suited for survival in stochastic environments such as tailwater fisheries, but spumaline producing glands are absent from Ephemeroptera, Plecoptera, and most Coleptera (Matsuda 1976). Empheroptera and Plecoptera are among the most popular taxa used as indicators of biologic health in freshwater ecosystems and are being extirpated from tailwaters at an alarming rate (Vaikasas et al. 2013, Holt et al. 2015, Kennedy et al. 2016).

Hydropeaking as a novel environmental filter and driver of insect community structure

Flowing waters are among the most complex and dynamic ecosystems on Earth, and they harbor diverse communities of organisms that have evolved myriad morphological, behavioral and life-history adaptations in response to natural flow conditions (Naiman et al. 1993, Dynesius and Nilsson 1994). When natural flows are altered, organisms may not have the required traits or behaviors needed to persist under the alternative hydrologic regime. Species with complex life cycles requiring specific sets of conditions at multiple life stages will be especially susceptible to detrimental effects (Smith et al. 2009, Alp et al. 2013). Loss of insects and other groups from tailwaters after dam construction is well documented (Ward and Stanford 1979, Power et al. 1996, Vinson 2001, Arthington et al. 2006). Our results, in combination with those of other researchers, demonstrate that successful insect recruitment in tailwaters could be heavily dependent upon flow conditions, and limitations to recruitment caused by hydropeaking could be one explanation as to why some insect taxa are extirpated from tailwaters while others persist. We present two novel mechanisms by which insect recruitment and, subsequently, community

546 structure may be altered by novel flow fluctuations: reductions in oviposition habitat availability
547 and increased risk of egg mortality due to desiccation.

548 Reductions in the total number of oviposition sites due to hydropeaking could have
549 severe consequences for populations of larval aquatic insects. Lancaster and Downes (2014)
550 found that numbers of early instar *Baetis rhodani* and *Rhyacophila dorsalis* were positively
551 correlated with the number of oviposition sites, in this case emergent rocks. Adults of both of
552 these species cement their egg masses to emergent rocks. Interestingly, numbers of *Simulium*
553 spp. larvae, whose adults lay eggs on trailing riparian vegetation, did not correlate to the number
554 of emergent rocks present, suggesting that differences in *B. rhodani* and *R. dorsalis* larval
555 numbers between reaches were due specifically to changes in the abundance of preferred
556 oviposition sites. More compellingly, Encalada and Peckarsky (2012) demonstrated that direct
557 manipulations to the abundance of emergent rocks across several stream reaches altered both egg
558 mass densities and larval abundances of *Baetis bicaudatus*. In reaches where all emergent rocks
559 were removed, egg densities dropped to zero and average larval densities declined by a factor of
560 almost 2.5 one year after the manipulations. In combination, these studies provide strong
561 evidence that availability of preferred oviposition habitats is more important to recruitment and
562 population sizes of aquatic insect larvae than previously thought.

563 Management of dam releases such as hydropeaking can essentially manipulate the
564 abundance of preferred oviposition sites, just as in Encalada and Peckarsky's experiment, only
565 on timescales that range from hours to days. Under commonly used double-peaking regimes,
566 river discharge increases in the hours around both dusk and dawn to generate electricity at peak
567 consumption hours, in turn raising stage height and altering the availability of oviposition sites.
568 Since dusk and dawn hours are believed to be the peak times for aquatic insect mating and

569 oviposition to occur (citations: Kriska et al 1998, others??), double-peaking flows have the
570 potential to negatively affect oviposition site availability and subsequent recruitment for insects
571 with edge-specialist, cementing behaviors. In addition to releasing water for generating power,
572 hydropeaking dams often conduct sustained high flow events (HFEs) for either reservoir water
573 storage or to mimic natural flooding. These high flow events can last anywhere from a few days
574 to several months, as was the case below FGD in 2017, when flows remained at or above 198 m^3
575 s^{-1} (more than 8x the minimum flow of 22.7 m^3 s^{-1}) for three months. If HFEs act to submerge
576 most or all oviposition sites during times of peak oviposition, insect recruitment could be
577 severely depressed. Regulated flows of any type essentially present ovipositing insects with a
578 "moving target" in terms of where and when optimal oviposition sites will be available. Over
579 time, repeated exposure to this novel pressure may act to extirpate taxa with rigid oviposition
580 behaviors that cannot adapt.

581 Researchers have suggested that these two recruitment limitations imposed by
582 hydropeaking operations could influence community structure by leading to the extirpation of
583 select insect taxa, specifically those considered as edge-specialists that utilize varial zone
584 habitats for oviposition (Kennedy et al. 2016). Both hydropeaking high and low flows have the
585 potential to reduce population recruitment, but by different mechanisms – loss of habitat and
586 desiccation, respectively. These mechanisms could very well explain the virtual dearth of
587 sensitive taxa from the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) in the Colorado
588 River tailwater below Glen Canyon Dam, as well as the depleted assemblages in other desert
589 tailwaters such as that below Hoover Dam. Hydropeaking regimes in these tailwaters are more
590 intense compared to the FGD tailwater (see Kennedy et al. 2016), with large disparities between
591 low and high flows on a regular, daily basis. Additionally, the canyon-bound geography of these

592 particular tailwaters means changes in discharge will translate to significant stage height
593 fluctuations in varial zone habitats, both submerging (negative for ovipositing adults) and
594 exposing (negative for egg masses) emergent particles more easily. This, in combination with
595 highly arid atmospheric conditions in the surrounding terrestrial landscape, creates a highly
596 stressful environment for both adults and egg masses of aquatic insects with edge-specialist,
597 cementing oviposition behaviors. In these specific systems, hydropeaking may artificially select
598 against these taxa, producing a depauperate insect community.

599 However, other tailwaters with hydropeaking regimes, such as that below FGD, contain a
600 relatively healthy assemblage of EPT taxa, which begs the question as to the relative strength of
601 these hydropeaking-induced recruitment constraints in shaping insect community structure. If the
602 regional species pool is comprised of taxa with relative plasticity in oviposition behaviors, these
603 communities may not be as affected by detrimental effects of fluctuating water levels on habitat
604 availability. For example, while all previous research found *Baetis spp.* oviposition to occur
605 almost entirely on emergent rocks (Eaton 1888, Peckarsky et al. 2000, Encalada and Peckarsky
606 2006, Encalada and Peckarsky 2012), we found *Baetis* egg masses on a variety of substrates,
607 including *Typha* reeds, pine cones and bark and willow branches. The ability for *Baetis* in this
608 study to oviposit on a variety of substrates may help ensure recruitment for this taxon at times
609 when flows significantly reduce the abundance of preferred substrates. Similarly, if the regional
610 pool consists of taxa with oviposition behaviors that are not as susceptible to negative effects of
611 altered flows, such as the swimming behaviors of *H. occidentalis*, extirpations may not be as
612 widespread.

613

614 *Suggestions for large river management*

River managers and dam operators are increasingly interested in balancing societal power needs with the ecological integrity of tailwaters and the flora and fauna that inhabit these ecosystems. Given the potential for hydropeaking flows to alter the spatial and temporal existence of optimal oviposition habitats, as well as to increase the risk of mortality for unhatched eggs, it is important to consider how management practices could be used to mitigate the negative effects of altered flows on processes occurring during non-larval insect life stages. The most straightforward method to diminish the effects of hydropeaking on adult oviposition and egg mass hatching is to reduce hydropeaking flows during periods of intense oviposition. Most uni- and multi-voltine aquatic insects oviposit during spring and summer months (citations), so reducing the disparity between high and low daily flows during these periods of the year would undoubtedly help to alleviate the potential detrimental effects of hydropeaking mentioned thus far. Similarly, running lower flows during daily peak oviposition hours would increase the chances of egg masses being laid at low stage heights, thus remaining submerged during higher flows. It is thought that most aquatic insects oviposit near dawn and dusk hours (citations). Unfortunately, morning and evening hours are precisely the times of day when electricity demand is often highest and hydropeaking flows are implemented. Therefore, this method seems unlikely. Instead, more stable, lower flow regimes implemented for short periods during peak oviposition, such as the low weekend flow regime suggested by Kennedy et al. (2016), may be more economically and sociably feasible. Regardless, solutions to recruitment constraints imposed by hydropeaking flows will require robust data sets on regional and local insect phenologies and cooperation between land managers, scientists, and the public.

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644

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797 **FIGURES**

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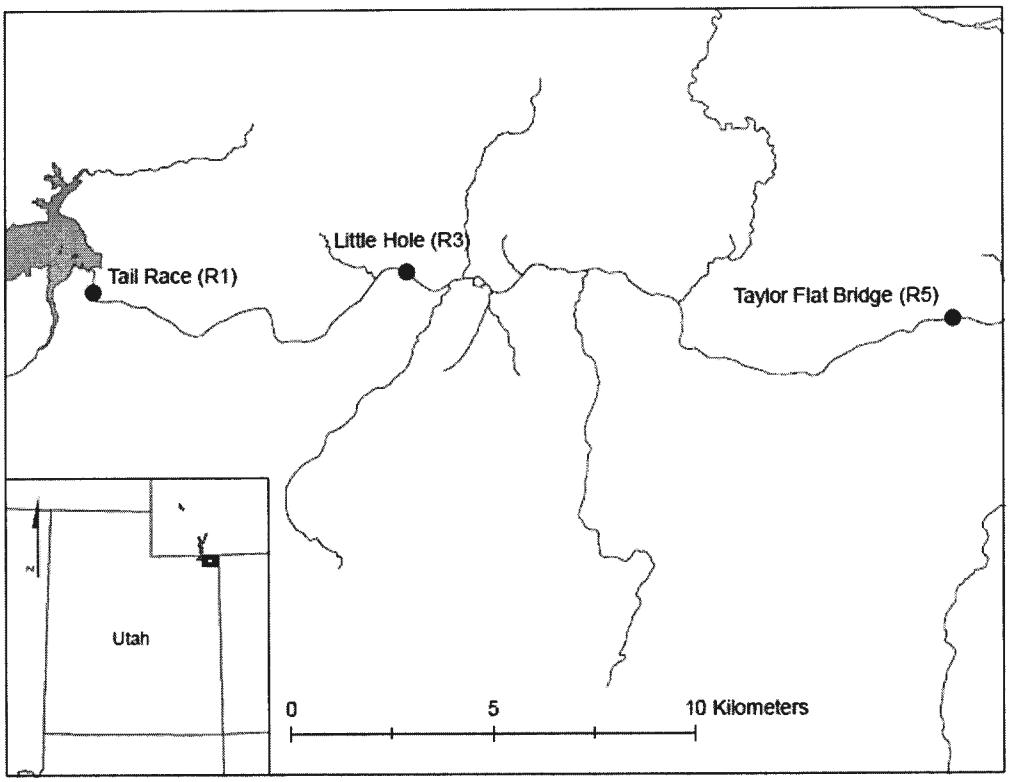

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802 Figure 1. Location of the Green River within Wyoming, Utah and Colorado. Shown are the three
803 study segments located below Flaming Gorge Dam: Tail Race, Little Hole and Taylor Flat
804 Bridge.
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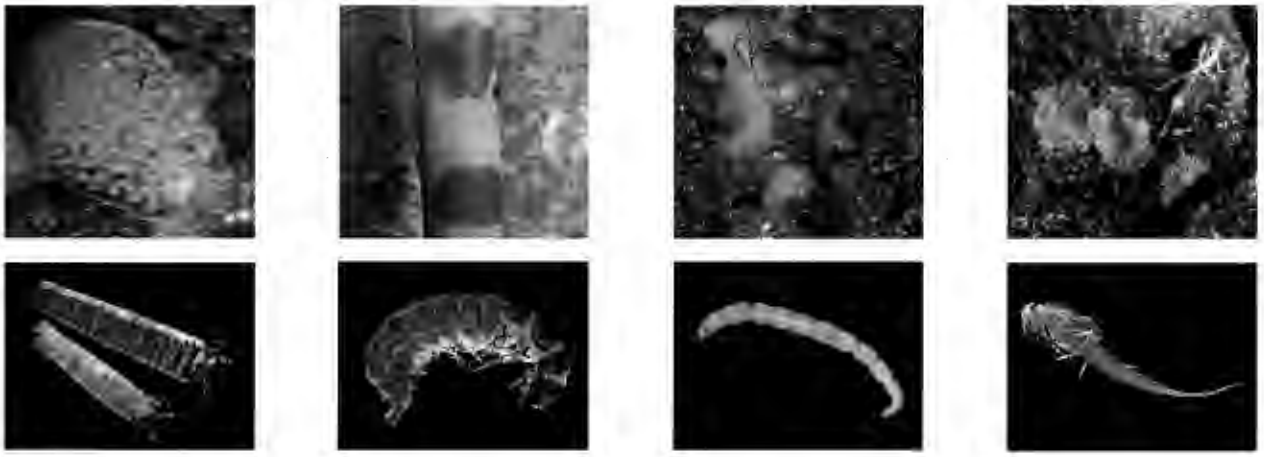

Figure 2. Larval and egg mass photos of *Brachycentrus occidentalis* (Trichoptera), *Hydropsyche occidentalis* (Trichoptera), Chironomidae (Diptera) and *Baetis* spp. (Ephemeroptera).

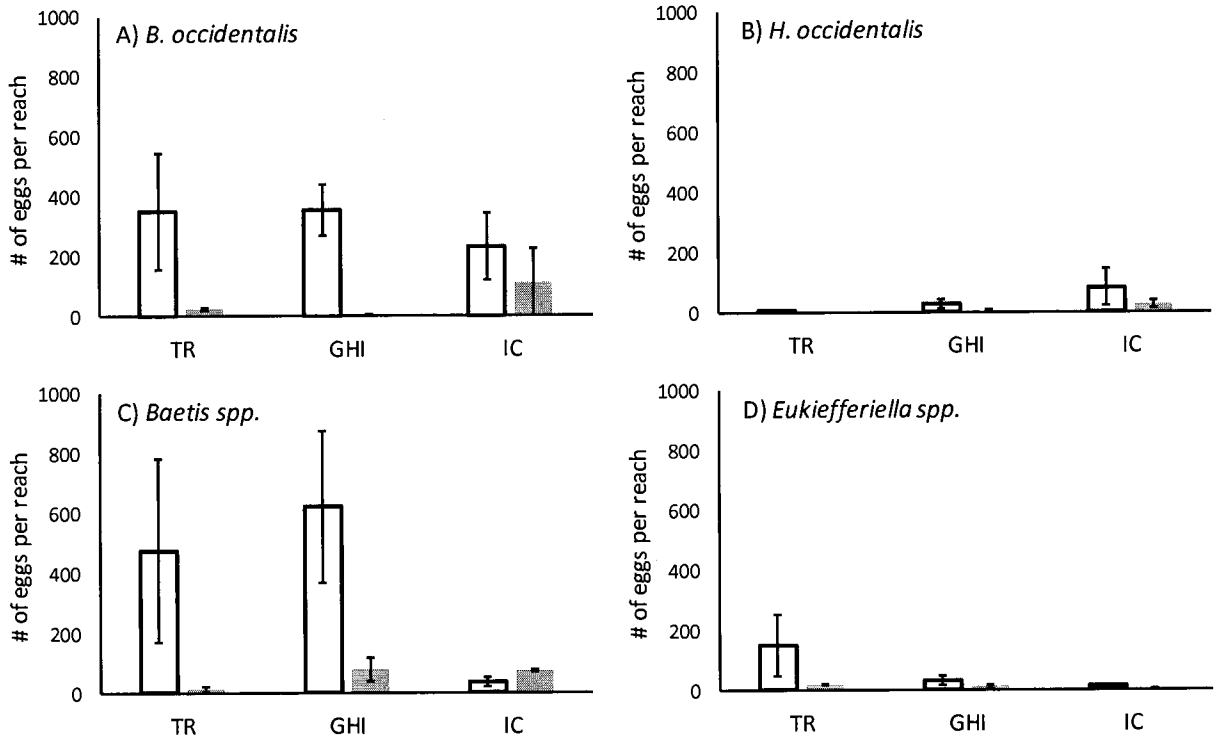

Figure 3. Average number of egg masses (± SE) per fast- (open bars) and slow-water (closed bars) reach compared among each of the three study segments for A) *B. occidentals*, B) *H. occidentalis*, C) *Baetis* spp. and D) Chironomidae.

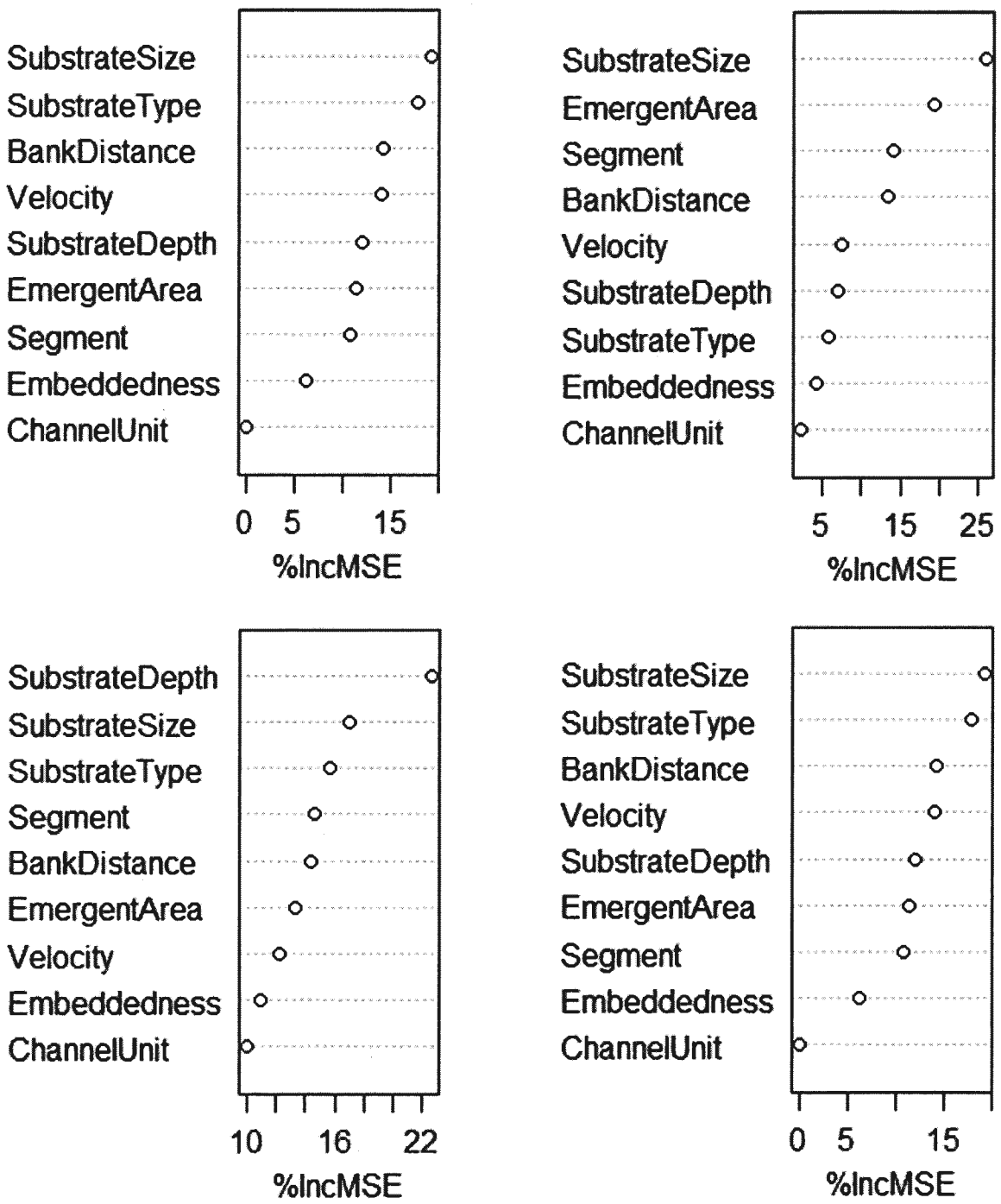

Figure 4. Variable importance plots for the random forest models developed to understand relationships between oviposition egg density and environmental conditions for *B. occidentalis* (top left), *H. occidentalis* (top right), Chironomidae (bottom left) and *Baetis* spp. (bottom right). The sensitivity of egg density to individual predictors was assessed by quantifying the percent increase in mean square error (%IncMSE) when the validation data for an individual predictor was permutated.

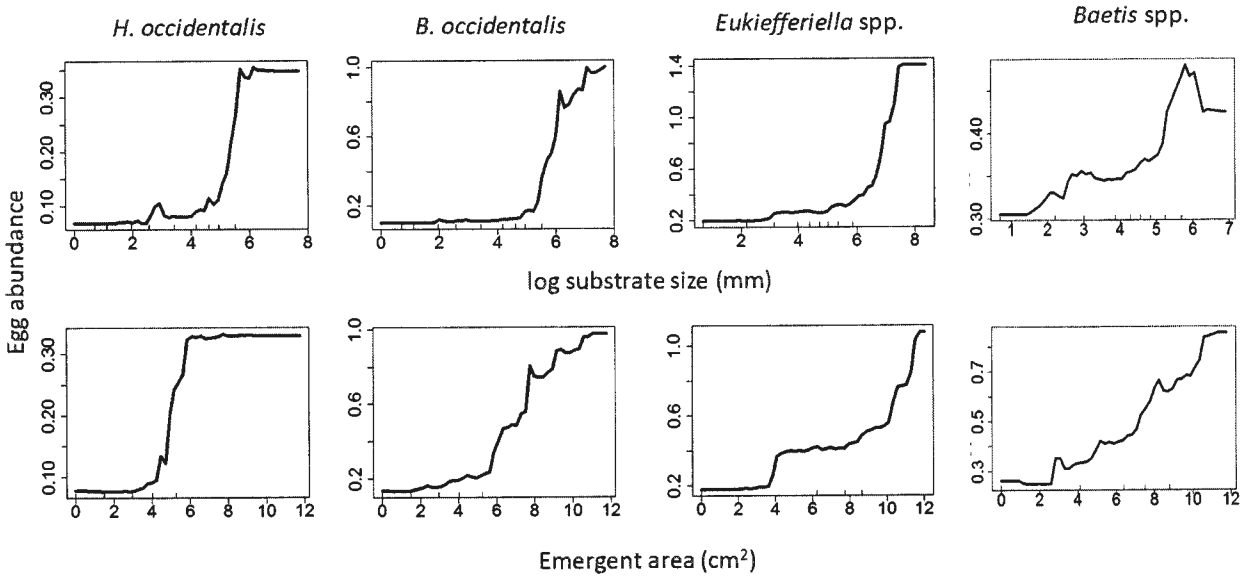

Figure 5 Partial dependency plots of *H. occidentalis*, *B. occidentalis*, Chironomidae and *Baetis* spp. egg densities exhibiting similar relationships with substrate size and emergent area from each of the four independent Random Forest models. All four taxa show preferences for large, emergent substrates.

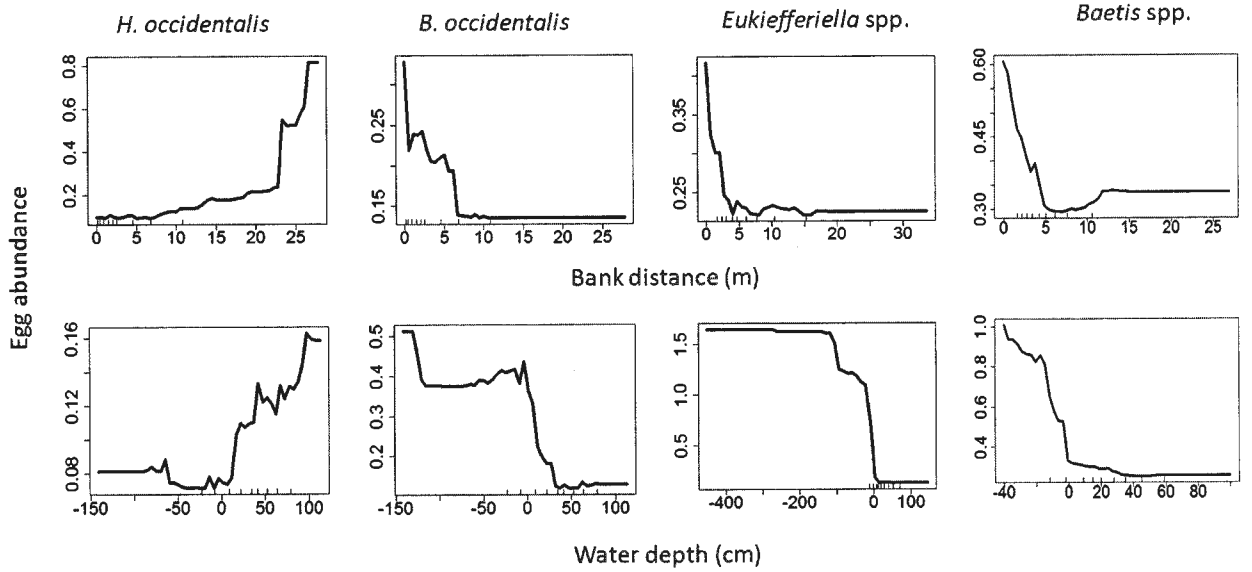

Figure 6. Partial dependency plots of *H. occidentalis*, *B. occidentalis*, Chironomidae and *Baetis* spp. egg densities exhibiting differential relationships with bank distance and water depth from each of the four independent Random Forest models. *B. occidentalis*, Orthocladiinae and *Baetis* spp. exhibited similar relationships, while *H. occidentalis* differed. Negative values for water depth represent egg mass that were above water during the surveys (i.e., surveys were conducted at daily low flows and these egg masses were likely laid at daily high flows).

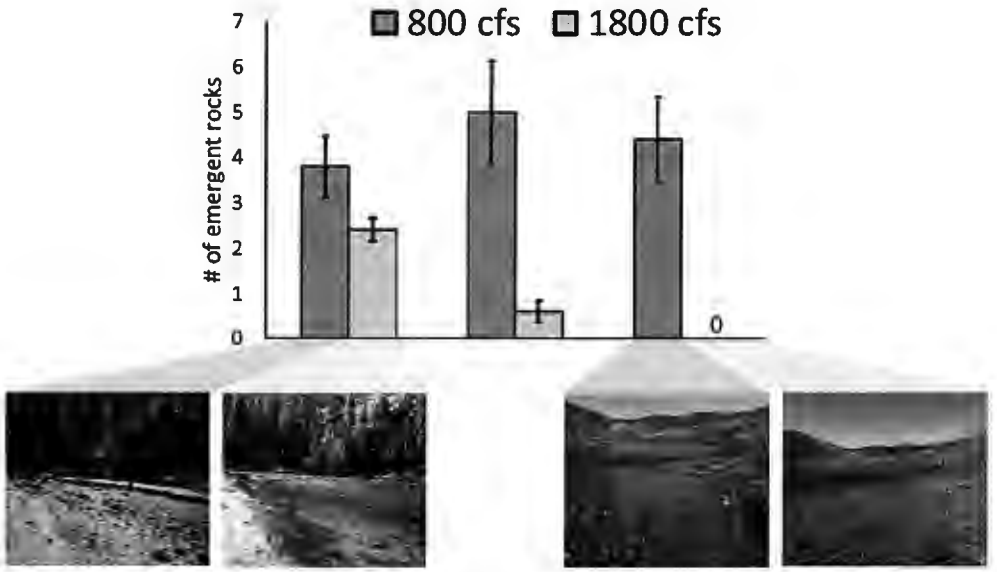

Figure 7. Average number of emergent rocks found during random surveys compared between 800 and 1800 cfs for Tailrace, Grasshopper Island and Indian Crossing study segments.

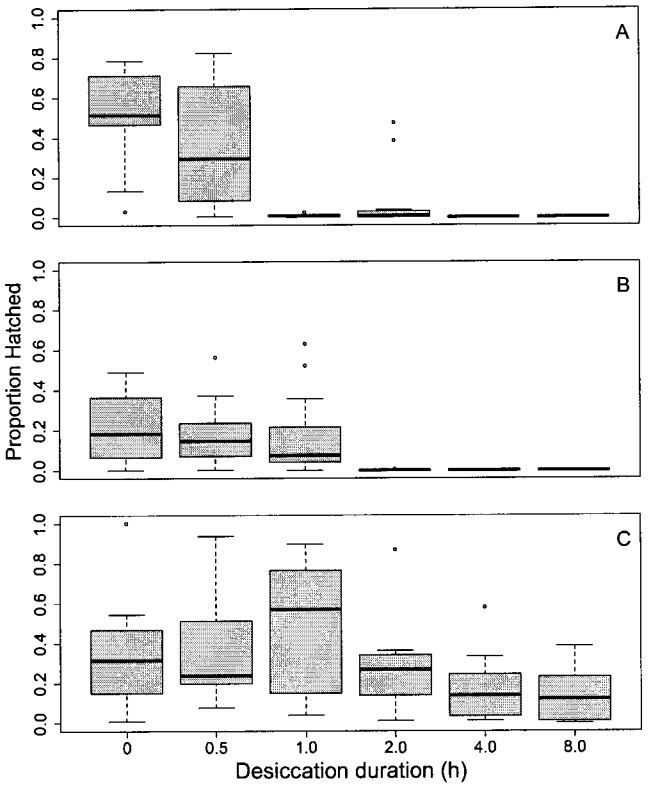

Figure 8. Proportional hatching success compared among a control and five levels of desiccation for (A) *Baetis* spp., (B) *Hydropsyche occidentalis* and (C) *Brachycentrus occidentalis* egg masses.

Table 1. Measured physical habitat variables used to characterize both habitat availability and habitat utilization by ovipositing invertebrates in the tailwater of the Green River, Utah, USA.

1. Segment scale - location of ovipostion substrate within study segment
1.1 Reach type (fast or slow)
2. Reach scale - location of substrate within study reach
2.1 Distance from bankfull (m)
3. Substrate scale - characteristics of substrate
3.1 Type (emergent rock, submerged rock, emergent wood, submerged wood, or emergent vegetation)
3.2 Size (mm; b-axis or max. diameter for mineral or organic substrates, respectively)
3.3 Particle depth (cm)*
3.4 Emergent area (cm^2)
3.5 Water velocity at 60% water depth and immediately upstream of substrate; measured in bins: <0.06; 0.06 - 0.25; 0.26 - 0.50, 0.51 - 1.00; and >1.00 m^3 sec^{-1}
3.6 Embeddedness: <10, 10 - 40, 41- 75, and >75%

* Measured as distance from water surface to top of particle; negative value indicates height of emergent particle above water

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Reflection:

Conducting research as an undergraduate can be a challenging experience, where some students have a natural talent for forming questions and carrying out experiments. While other undergraduates might have to learn how to think analytically, being mindful of their influence on a project's outcome. To some extent, I believe I have traits and qualities from both of these groups.

I was fortunate enough to have found a job at the National Aquatic Monitoring Center (NAMC) early in my freshman year at Utah State University. I was a laboratory technician, working with aquatic macroinvertebrates (insects). At the time, I did not have much interest in entomology but felt the experience was too good to pass up and that I would start looking for a different position after six months. I stayed at the lab for all four years of my undergraduate career. My research experience with NAMC began at the start of my 2nd year when I approached the lab director, Dr. Scott Miller, about being a summer field technician. Quickly, he gaged my interest and sat me down with an inch-thick stack of scientific papers which outlined the project in great detail. I was to join a small team of researchers with the proposed goal of re-examining how society views a renewable resource, hydroelectric power. Over the past three years, I have found that hydropower is sustainable in the context of producing electricity but not ecologically.

My first major struggle was trying to "catch up" with my colleagues who had been on this project and in the field for years prior to my start. It seemed like I would never reach their level of understanding. It still doesn't, but I know now that individuals apart of a team do not need to know everything. Rather, everyone has an individual area of expertise that can contribute to the greater project goal. In time my expertise would revolve around insect eggs, everything from

their physiology and anatomy to their ecology and conservation. Its an odd niche to fill but it is rewarding to have peers seek you out for assistance.

The project itself entail week long trips to the Green River where I would collect larval insects as well as their eggs for experiments. Floating rivers is a phenomenal way to spend a summer, but it was coupled with week long periods, setting and observing egg development under various environmental conditions. Most researchers talk about how great the field aspect of their jobs can be but fail to mention how much time is spent inside a hot lab space during summer days. It was during those long lab days that I realized how fully immersed I was with this project and with the research process as a whole. I was enamored by the physically exhausting days and mentally exhausting nights, I felt like a workaholic and I loved it because I was trying to make a difference. I wanted to contribute to the well-being and sustainable management of environments at a large scale and that is exactly what I was doing.

I came to college with little to no understanding of what I really wanted from my next four years, I will be leaving Utah knowing exactly where I want to end up. Getting involved with both undergraduate research and clubs as a freshman allowed me to flourish as a student. It challenged me to explore different fields, work with new people, and push myself to succeed. While at USU, I successfully completed four research projects that were independent of each other and partially worked on two others. I discovered what I was passionate about by trying to do anything and everything that came my way. Water chemistry, geomorphology, climate physics, and aquatic ecology are just a few of the bigger themes that were covered by these projects. I knew very little about any of those topics prior to working with them but nothing can beat 1st hand experience. My biggest piece of advice to 1st year's is to push yourself outside your comfort zone because that is where you will learn something new about yourself or the world around you.

Biography

Jesse Fleri is a fourth-year student pursuing a B.S. in Conservation and Restoration Ecology with double minors in fisheries science and soil science. He will graduate with honors in the spring of 2018 having completed four research projects on a variety of natural resources topics. He has conducted research with physicists in a radiocarbon dating lab, environmental engineers assessing wastewater treatment standards, aquatic entomologists investigating life history bottlenecks in macroinvertebrate communities and geomorphologist modelling salt marsh morphodynamics in restored Chesapeake Bay islands. Jesse has been fortunate in his research pursuits, having participated in the NSF funded EPSCoR iUtah fellows programs as well as the NSF funded Maryland Sea Grant Research Experience for Undergrads (REU) fellows program. Jesse has presented oral and poster presentations at several conferences and recently had work he co-authored accepted for presentation at the European Geoscience Union. He is currently in the process of preparing two manuscripts for publication in peer-reviewed journals. Jesse will be pursuing a M.Sc. in Forestry at the University of British Columbia in conservation planning, community ecology, and spatial ecology of invasive species. He was award the college wide and university wide awards for Undergraduate Researcher of the Year in 2018.